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Taxonomic remarks on *Rhabdolepis saarbrueckensis* Gardiner, 1963 (Osteichthyes: Actinopterygii) and its relationships to some actinopterygians from the Late Carboniferous of the Bohemian Massif, Czech Republic

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Abstract. The newly discovered material of *Rhabdolepis saarbrueckensis* Gardiner, 1963 is described and the relationships to other species of the genus *Rhabdolepis* are discussed. The data obtained in the course of the study of the type specimens related to the species of *Rhabdolepis* makes possible a comparison with some actinopterygians of the Late Carboniferous of the Bohemian Massif.
Keywords. Actinopterygii, Permian, Carboniferous, Saar-Nahe Basin, Bohemian Basins

INTRODUCTION

An interesting set of specimens from the spherosiderite nodules of the Saar-Nahe Basin is found among the specimens from the Permo-Carboniferous basins of the Bohemian Massif in the collection of the National Museum, Prague, Czech Republic (NMP). They have been studied in the context of similarity of the actinopterygians of the Krkonoše Piedmont Basin and Saar-Nahe Basin within the framework of the Grant Project DE0604OMG003. The relatively well preserved specimen of the rare species *Rhabdolepis saarbrueckensis* Gardiner, 1963 is one of them.

Genus *Rhabdolepis* has a complicated history. The type species of the genus *Rhabdolepis* is *Rhabdolepis macropterus* (Bronn, 1829), which was originally described by Bronn (1829) as *Palaeoniscum macropterum*. Agassiz (1833: 31-35) transferred it to the genus *Amblypterus* Agassiz, 1833, at the same time describing in the latter genus the following species as new: *A. eupterygius* Agassiz (1833: 36-37), *A. latus* Agassiz (1833: 37-38), *A. lateralis* Agassiz (1833: 39), and *A. olfersi* Agassiz (1833: 40). In the supplement Agassiz (1833) added *A. agassizii* Münster (p. 105-106), *A. nemopterus* Agassiz (1833: 107-109), and *A. striatus* Agassiz (1833: 111-112).

It is important that Troschel (1857) considered the genus *Amblypterus* heterogeneous. He retained the species *A. latus* and *A. lateralis* with the brushing teeth and smooth

scales in the genus *Amblypterus*, whereas he erected the new genus *Rhabdolepis* for the species with large conical teeth and sculptured scales. Genus *Rhabdolepis* in the sense of Troschel (1857: 18) is characterized by the large conical teeth in a single row, brushing teeth on the palatine and by thick and striated scales. Sauvage (1888: 59) later designated *Rhabdolepis macropterus* (Bronn, 1829) as the type species of *Rhabdolepis*. The genus *Rhabdolepis* was re-described by Traquair (1877). Woodward (1891) transferred *Rhabdolepis macropterus* and *Rhabdolepis eupterygius* to the genus *Elonichthys* Giebel, 1848. Aldinger (1937) considered *Rhabdolepis* as a separate genus close to *Elonichthys*, and included it in his new family Elonichthyidae. Gardiner (1963) revised the genus *Rhabdolepis*, created a new family Rhabdolepidae Gardiner, 1963 for it, and described differences between the families Rhabdolepidae and Elonichthyidae. Gardiner (1963) provided a new diagnosis for *Rhabdolepis* and for *R. macropterus*, in which he included *R. eupterygius*. At the same time Gardiner (1963) designated specimen BMNH P 3453 (part and counterpart) from the collection of the Natural History Museum, London, as the neotype of *R. macropterus*, and described *Rhabdolepis saarbrueckensis* Gardiner, 1963 on the basis of the holotype BMNH 32576. The latter species differs from *R. macropterus* in the presence of two accessory operculars (instead of one in *R. macropterus*) and four ridge scales in front of the dorsal fin (instead of three in *R. macropterus*).

Heyler (1976) restudied the type of *Amblypterus eupterygius* figured by Agassiz (1833, Pl. 3, Fig. 6) and transferred it to genus *Watsonichthys*, remarking on its close resemblance to *Watsonichthys pectinatus* (Traquair, 1877). Boy (1976) figured scales of *Rhabdolepis macropterus*. He considered *Rhabdolepis eupterygius* as identical with *Rhabdolepis macropterus*, and indicated that *Rhabdolepis saarbrueckensis* may be only a variant of *R. macropterus*.

Schindler (in Poschmann & Schindler 2004) provided a new diagnosis for the family Elonichthyidae, in which he included *Elonichthys* Giebel, 1848, *Rhabdolepis* Troschel, 1857 and *Meisenheimichthys* Schindler, 2004. Schindler (2007) included in *Rhabdolepis R. macropterus* and *R. saarbrueckenensis*, whereas he transferred *R. eupterygius* to the genus *Elonichthys*. The reasons for the latter act are as follows (Schindler 2007): occurrence of the accessory opercular of triangular shape among the preopercular, opercular and subopercular (*Rhabdolepis* has one or two accessory operculars of oblong shape and completely separated opercular from the subopercular); maxillary plate quadrangular, relatively high (*Rhabdolepis* has low anteroposteriorly elongated maxillary plate); anterior margin of the preopercular is moderately concave (*Rhabdolepis macropterus* has anterior margin twice scalloped). Schindler (2007) pointed out the presence of only two specimens of *Rhabdolepis saarbrueckensis,* and such features as completely separated opercular and subopercular by two accessory operculars, which range the species to *Rhabdolepis*, and relatively high quadrangular maxillary plate which express the feature of *Elonichthys*.

A newly discovered specimen of *Rhabdolepis saarbrueckensis* from the collection of the National Museum, Prague, supplements our knowledge of this rare species. Below I present results of my study of the latter specimen, and of its comparison with other

species of the genus *Rhabdolepis*, and with some related actinopterygians from the Late Carboniferous of the Bohemian Massif.

MATERIAL AND METHODS

All *Rhabdolepi*s specimens originated from the Lebach limonite-siderite nodules of the Saar-Nahe Basin (Meisenheim Formation, M 10 Humberg-Bank in the sense of Boy 1994). The specimen NMP Sc 95 is deposited in the National Museum, Prague. The type specimens of *R. saarbrueckensis*, *R. macropterus* and *R. eupterygius* are deposited at the Natural History Museum, London (BMNH), at the Université de Strasbourg (VP) and at the Staatliches Museum für Naturkunde, Stuttgart (SMNS). The specimens from spherosiderite nodules of the Late Carboniferous of the Bohemian Massif are deposited at the National Museum, Prague and at the Museum of Western Bohemia at Plzeň (M). The uncatalogued type specimen of *Elonichthys crassidens* is deposited in the Martin-Luther-Universität Halle/Saale.

Descriptive terminology conforms to that adopted by Grande & Bemis (1998) with inclusion of some terms and methods of observations, drawings and measurements according to Štamberg (2007).

SYSTEMATIC PALEONTOLOGY

Subclass Actinopterygii Cope, 1887

Family Rhabdolepidae Gardiner, 1963

***Rhabdolepis saarbrueckensis* Gardiner, 1963**

1963 *Rhabdolepis saarbrueckensis* n. sp. Gardiner, p. 289-290, Fig. 10
2007 *Rhabdolepis saarbrueckensis* Gardiner 1963; Schindler, p. 245

Holotype: Specimen BMNH 32576 (part and counterpart), deposited at the Natural History Museum, London.

Material: Specimen NMP SC 95, deposited at the National Museum, Prague.

Description:

The following description focuses exclusively on the specimen Sc 95. The preserved part in the spherosiderite concretion is 31 cm long, although the estimated total length of the specimen is 34 cm. The outline of the body, scales, anal fin, most of the caudal fin, opercular bones, bones of the skull roof and supracleithrum are preserved (Figs. 1, 2).

Partly preserved impression of the skull roof exposes the anteroposteriorly elongated frontal with a trace of the supraorbital canal. The anterior concave border of the right and left frontals creates the space for the postrostral. The dermosphenotic borders the right frontal, and it separates the frontal from the orbit. Indistinct impressions of the parietals posterior to the frontal are in the place of otoliths. Postrostral is preserved separately from the skull roof. Posterior margin of the bone is convex, and surface of the posterior part of the bone is sculptured with anteroposteriorly oriented striae.

A fragment of the quadrate and impression of the pterygoidal bones, namely the dermometapterygoid, the ectopterygoid and the entopterygoid are seen (Fig. 3). Entopterygoid

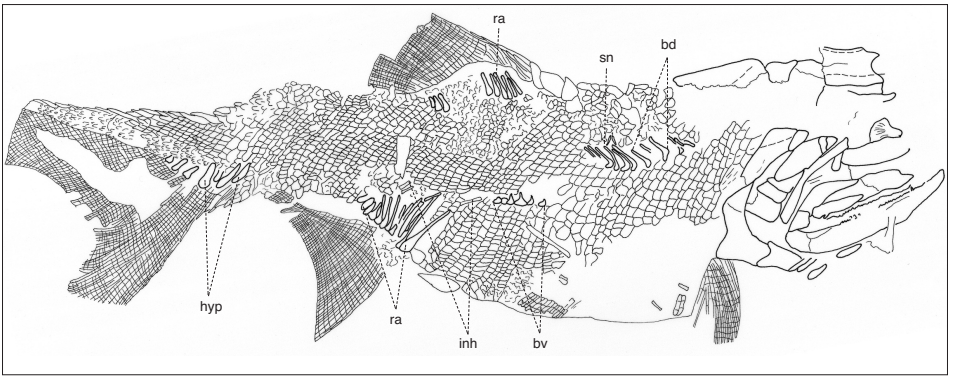

Fig. 1. ***Rhabdolepis saarbrueckensis*** **Gardiner, 1963. Interpretive drawing of the whole specimen Sc 95. Compare with the Fig. 2. The position of the rests of the axial skeleton are marked, × 0.4; bv – basiventral; bd – basidorsal; hyp – hypural, inh – intrahaemal; ra – radial; sn – supraneural.**

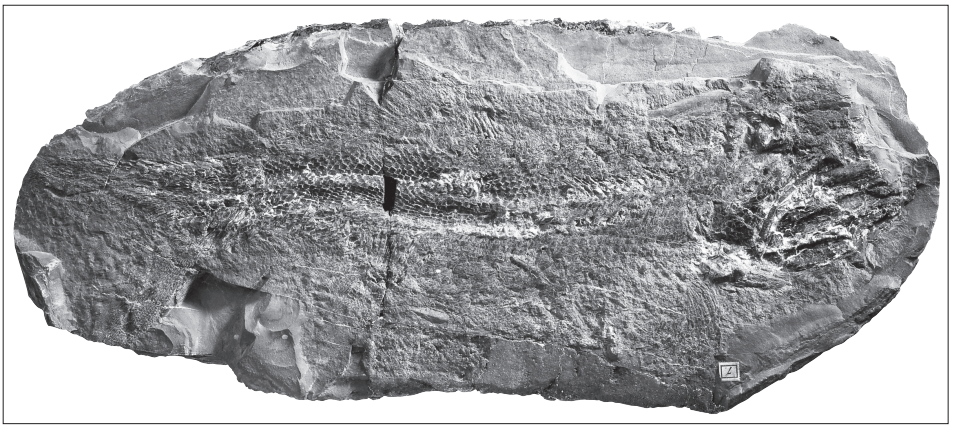

Fig. 2. ***Rhabdolepis saarbrueckensis*** **Gardiner, 1963. Nearly whole specimen Sc 95 from the locality Lebach, × 0.4.**

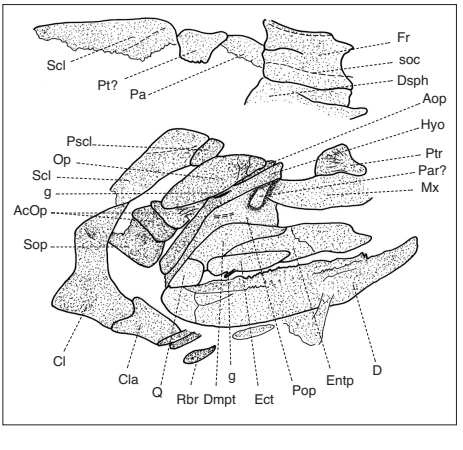

Fig. 3. ***Rhabdolepis saarbrueckensis*** **Gardiner, 1963. Interpretive drawing of the head in lateral view. Sc 95, × 0.7. AcOp – accessory opercular; Aop – antopercular; Cl – cleithrum; Cla – clavicle; D – dentary; Dmpt – dermometapterygoid; Dsph – dermosphenotic; Ect – ectopterygoid; Ent – entopterygoid; Fr – frontal; g – groove; Hyo – hyomandibular, Mx – maxillary; Op – opercular; Pa – parietal; Par? – processus ascendens of the parasphenoid; Pop – preopercular; Pscl – presupracleithrum; Ptr – postrostral; Q – quadrate; Rbr – branchiostegal ray; Scl - supracleithrum; soc – supraorbital canal; Sop – subopercular.**

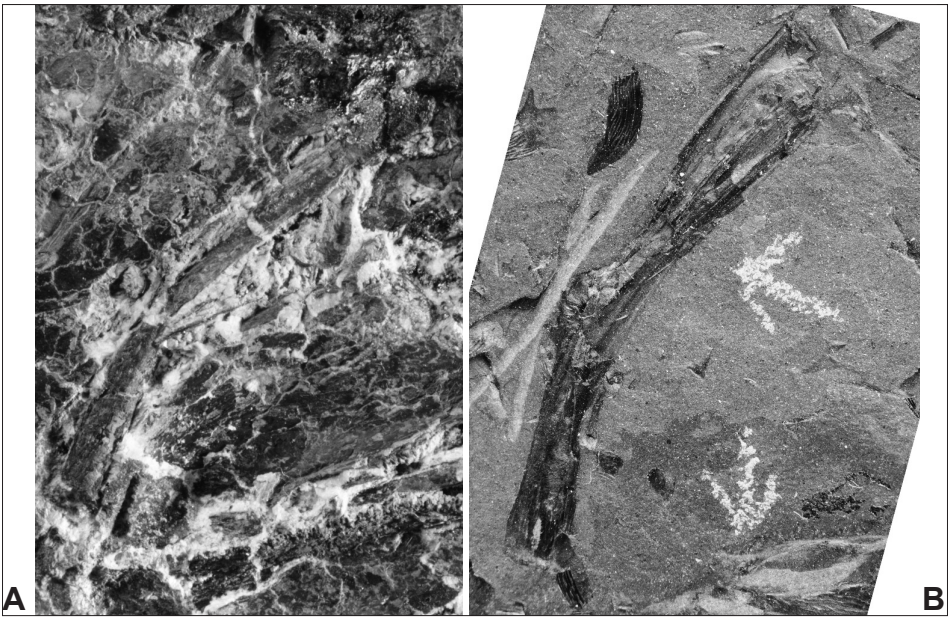

Fig. 4. A, *Rhabdolepis saarbrueckensis* Gardiner, 1963. Right hyomandibular in lateral view, Sc 95, × 2. B, *Elonichthys crassidens* Giebel, 1848. Right hyomandibular in lateral view. The type specimen without number deposited at the Martin-Luther-Universität Halle (Giebel 1849, Pl. 30, Fig. 6), × 2.

is the largest bone of the medial side of the palatoquadrate. It posteriorly borders with the dermometapterygoid, and posteroventrally with the ectopterygoid. The ectopterygoid is restricted to the posterior area of the palatoquadrate. It is much shorter than this bone on *Pteronisculus aldingeri* (Nielsen 1942, Fig. 37), and not as large as on *Mimia toombsi* (Gardiner 1984, Fig. 54). Numerous minute and stout teeth are preserved along the ventral border of the ectopterygoid. The ectopterygoid carries a narrow groove along the ventral border of the bone. The groove continues on the small laterally protruding processus ectopterygoideus. Gardiner (1984) described a similar narrow groove along the ventral border of the ectopterygoid transversing to the dermopalatines in *Mimia toombsi*. The groove in our case turns laterally to processus ectopterygoideus similarly to that figured by Aratia & Schultze (1991, Fig. 9b) in *Polypterus ornatipinnis*.

The preopercular borders the upper jaw posteriorly and dorsally. Indistinct outline indicates conspicuous inclination of the preopercular anteriorly, and the presence of the preopercular canal conserved in the place of the bend of the bone.

Very stout hyomandibular protrudes between the preopercular and the opercular. It is a dorsoventrally elongate bone bent conspicuously just in the middle of its length. The bend divides the bone into a distinctively anteriorly inclined branch and a ventral branch which is in a nearly dorsoventral position (Fig. 3). Anterior and ventral branches of the hyomandibular form an angle of 152 degrees. Ventral very stout branch is circular in cross-section, anterior branch is lateromedially flattened and gradually broadening

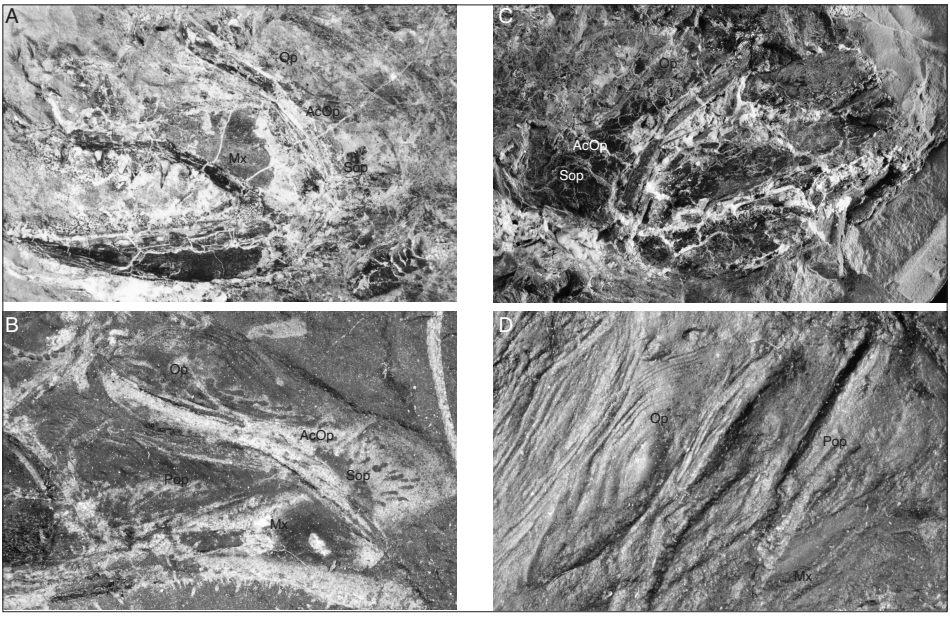

Fig. 5. Bones of the opercular apparatus and the cheek in lateral view. A, *Rhabdolepis macropterus* (Bronn, 1829), BMNH P3453, × 0.6; B, *Rhabdolepis macropterus* (Bronn, 1829), BMNH P 6196, × 1.3; C, *Rhabdolepis saarbrueckensis* Gardiner, 1963, Sc 95, × 0.9; D, *Rhabdolepis eupterygius* (Agassiz, 1833), SMNS 95379, × 5.2. AcOp – accessory opercular; Mx – maxillary; Op – opercular; Pop – preopercular; Sop – subopercular.

anteriorly. Posterior margin of the bone produces into a rounded, not particularly prominent processus opercularis in the place of the bend of the hyomandibular. A conspicuous narrow groove starts at the level of processus opercularis, and gradually broadens and shallows in the dorsal direction. This groove can be compared with the canal for truncus hyoideomandibularis facialis (Nielsen 1942) in *Pteronisculus magnus* (Nielsen, 1942). Besides its robustness, the hyomandibular is distinguished by its bend, which is much more noticeable than those figured by Nielsen (1942) in *Pteronisculus magnus*, Aldinger (1937) in *Pygopterus nielseni* or Poplin & Veran (1996) in *Coccocephalus wildi*. The shape of the hyomandibular, including of the bend of the bone and the shape of processus opercularis corresponds to that in *Meisenheimichthys palatinus* (Schindler, 1993). Correspondence in the angle of the bend can be found also with the type specimen of *Elonichthys crassidens* Giebel, 1848 (personal observation). The angle of the bend of the hyomandibular of *E. crassidens* is 145 degrees, but the ventral branch is about 1/3 shorter than the dorsal one (Fig. 4).

Only a fragment of the stout lower jaw is preserved. The lower jaw is equipped with numerous small teeth, and only one fragment of 3 mm long tooth remained of the conical teeth.

The opercular, two accessory operculars, the subopercular and fragments of the branchiostegal rays are preserved. The opercular is distinctively dorsoventrally elongated

bone. It is very narrow, widest in its dorsal area, and gradually narrows ventrally. The ventral end is rounded. The opercular is markedly inclined anteriorly at an angle of 36 degrees. A small antopercular lies anteriorly to the dorsal part of the anterior margin of the opercular. Two accessory operculars and subopercular are positioned ventrally to the opercular. Accessory operculars are narrow bones separating opercular from the subopercular. The dorsally lying accessory opercular is slightly narrower than the second one lying ventrally. The anterodorsal margin of the accessory opercular lying ventrally from the opercular is not well preserved, but nothing indicates that the area anteriorly to the narrow ventral part of the opercular was filled in with a separate bone, as it is in several other genera (*Watsonichthys, Cosmoptychius, Meisenheimichthys* etc.). This area was probably filled in with anterior broadened part of the accessory opercular. A small subopercular of oblong shape is larger than the preceding accessory opercular. Probably numerous branchiostegal rays were present, but fragments of only three branchiostegal rays are preserved.

The supracleithrum, the presupracleithrum, the cleithrum and the clavicle are exposed from the dermal bones of the pectoral girdle. The supracleithrum is a narrow, dorso-ventrally elongated bone, narrowing in ventral direction. Its ventral end is rounded and reaches the subopercular. Marks of the lateral sensory canal are recognizable in the dorsal third of the bone. A small presupracleithrum of an elliptical shape inserts between the dorsal area of the supracleithrum and the dorsal area of the opercular. Fragmentarily preserved cleithrum reaches with its dorsal pointed end to the accessory operculars; its wide anteroventral convex margin fits in the concave posterior border of the clavicle. The boundary of both bones is at the level of the anterior border of the subopercular.

Specimen Sc 95 exposes numerous ossifications of the axial skeleton. They are partly preserved in the anterior region of the trunk and in the abdominal region. The position of the vertebral column is discernible by a disruption of the scales of the lateral side of the body. The dorsal row of basidorsals and the ventral row of basiventrals are distinguished by their position in the anterior region of the trunk. There are nine basidorsals (Fig. 1) consisting of broadened basal areas and long distal processes in dorsoposterior direction. The long processes have their distal end slightly spread. The distal ends of the basidorsals are connected to the slender supraneurals. Only two supraneurals are partly preserved, the other are under cover of the scales. The basiventrals occur as robust ossifications of triangle shape arrange in the row. The basiventrals are in larger part under cover of the scales, and they only partly emerge to the surface. The robust distal parts of the hypurals are along the base of the ventral lobe of the caudal fin (Fig. 1). The position and the shape of the basidorsals and the supraneurals correspond with these bones figured by Nielsen (1942, Figs. 48, 50) in *Pteronisculus magnus*. The distal ends of the basidorsals in *Pteronisculus magnus* are considerably broader than those in *R. saarbrueckensis*.

The endoskeleton of the pectoral fin is unknown, also the number of the lepidotrichia of the pectoral fin. The numerous lepidotrichia of the pectoral fin are segmented from their base besides the base of the lepidotrichia of the leading edge of the fin. They are not articulated approximately to the first third of their length. The leading lepidotrichium

of the fin carry numerous very small fulcral scales. The pectoral fin is not entirely preserved, neither on this specimen nor on the holotype BMNH 32576, and the exact shape and size of the fin is impossible to determine. We can only suppose the same size as in *R. macropterus*.

The whole anal fin, nearly the whole the caudal fin and part of the dorsal fin are preserved from the unpaired fins. The anal fin is large, distinctly triangular, and concave posteriorly. The length of the base of the fin matches the length of the leading edge of the fin. The anal fin consists of at least 35 articulated lepidotrichia, and the longest lepidotrichia have more than 20 segments. The segments are short and wide. The leading edge has small and numerous fulcral scales. The endoskeleton of the anal fin consists of radialia. Fifteen radials are preserved, but their total number was higher. The radials in anterior position are long; they have a broad basis and a slender and long spine in the dorso-anterior direction. Diagonally antero-posteriorly arranged infrahaemalia are between the slender spines of anterior radials and supposed placement of the vertebral column.

Dorsal fin exhibits its base. It consists of about 35 articulated lepidotrichia. The segments are wide and short. The radials form the endoskeleton of the dorsal fin. The radialia have broad bases, narrowing distally, and broadening again on the distal end. The width of the basal area is each time greater that the distal one. Posteriorly situated radialia are shorter and wider than those in anterior region of the base of the fin. The radialia of the dorsal fin are markedly shorter that the radialia of the anal fin. Radialia of the anal fin are in their shape alike the radialia figured by Gardiner (1963, Fig. 8) in *Nematoptychius greenocki*. The radialia of the anal fin of *Pteronisculus* figured by Nielsen (1942, Fig. 50) have a broad basal area, longer than those in *R. saarbrueckensis*. Radialia of the anal fin in *Sceletophorus biserialis* are shorter, considerably broader on both ends (Štamberg 1983, Fig. 6).

The anal fin is deeply cleft with a well developed ventral lobe. The posterior ends of the dorsal and ventral lobes are missing.

The scales are small and numerous. The outer surface of the scales bears striae, which run from the anterior-superior corner to the posterior-inferior corner, but a little less steeply than the direction of diagonal. The posterior margin of the scales is denticulate. Four large scales precede the base of the dorsal fin. There is a single anteroposteriorly elongated large preanal scale, and paired large scales surrounded the anus in front of the anal fin. The squamation of the body is significantly distorted, but the approximate scale count is:

$$\frac{36}{12 \quad 33 \quad 59} \quad 64$$

Basic characters of *Rhabdolepis saarbrueckensis* Gardiner, 1963

Summarizing the features of the specimen NMP Sc 95 and the holotype BMHN 32576, the species can be characterized as follows:

Predatory medium-sized fish with fusiform body. The length of the head is 4.7-5 times and the height of the body is 3.7-4.3 times the total length of the body. The fins are large.

The pectoral fin with the lepidotricha articulated close their base, except for the three first lepidotrichia on the leading edge, which are not articulated in their first third of the length. Anal and dorsal fins triangular with their posterior margin concave. Anal fin consists of 41, and dorsal fin 35 lepidotrichia. All fins with minute and numerous fulcral scales. The scales on the body small, ornamented with striae, which run from the anterior-superior corner to the posterior-inferior corner. The striae occasionally anastomose posteriorly, and they pronounce to denticulation on the posterior margin of the scale. Four large ridge scales in front of the dorsal fin, single antero-posteriorly elongated ridge scale and a paired large scale in front of the anal fin. The scale count is:

$$\frac{36}{12\ \ 26\text{-}33\ \ 59} \quad 64?$$

The frontals are ornamented with tubercles, and they are not in touch with the orbit. Lower jaw stout, upper jaw with maxillary plate low and long. Numerous small teeth in one outer row, and less numerous large conical teeth in inner row on both jaws. The stout hyomandibular comprises anterior and ventral branches which form an angle of 152 degrees. Processus opercularis occurs in the place of the bend of the hyomandibular. The preopercular considerably inclines anteriorly, and it borders posteriorly and dorsally the maxillary plate. Two small suborbital bones are placed anteriorly to the preopercular. Small dorsoventrally elongated antopercular between the dorsal area of the opercular and dorsal area of the preopercular. The opercular narrow and considerably elongated dorsoventrally, ventrally narrowing (NMP Sc 95), or parallelogram shaped (BMNH 32576). Opercular considerably inclines anteriorly at an angle 36-40 degrees. Two accessory operculars of oblong shape completely separate the opercular from the subopercular. Branchiostegal rays numerous and small. Triangular presupracleithrum lies between the dorsal region of the opercular and the dorsal region of the supracleithrum. Narrow and considerably dorsoventrally elongated supracleithrum reaches up to the subopercular.

INTERSPECIFIC RELATIONSHIPS WITHIN THE GENUS *RHABDOLEPIS*

We know three species: *R. saarbruckenensis, R. macropterus* and *R. eupterygius* recurring in the history of the genus *Rhabdolepis. R. saarbrueckenensis* is discussed above.

***Rhabdolepis macropterus* (Bronn, 1829)**

This is the type species of the genus *Rhabdolepis*. The presence of the two accessory operculars in *R. saarbrueckensis* and one accessory opercular in *Rhabdolepis macropterus* is the basic diagnostic character distinguishing these two species. Gardiner (1963) designated this feature and it was confirmed with the present study. An additional diagnostic feature appears to be the shape of the opercular. The present study exhibit the narrow opercular, dorsoventrally elongated and narrowing ventrally as on *R. saarbrueckensis*, as in the type specimen BMNH P3453 and referred material (BMNH P6196) of *R. macropterus* (Fig. 5A, B). The shape of the opercular on the studied material is distinguished from that on the figures of *R. saarbruckensis* and *R. macropterus* presented by Gardiner (1963, Figs. 9, 10). The holotype of *R. saarbrueckensis* (BMNH 32576) has

parallelogram shaped opercular and Schindler observed (personal communication) the same shape of the opercular on the other specimens of *R. macropterus*. It is becoming apparent that the shape of the opercular can vary considerably.

The articulation on the leading edge of the pectoral fin is somewhat unclear. The lepidotrichia of the pectoral fin in *R. saarbrueckensis* are articulated from their base beside the first lepidotrichia, which are not articulated approximately to the first third of their length. The specimen BMNH M14537 of *R. macropterus* has all lepidotrichia articulated from their base. Regarding the low-level preservation of the leading edge of the pectoral fin on the studied specimens, the results of this study are in this respect unsatisfactorily verified.

***Rhabdolepis eupterygius* (Agassiz, 1833)**

Agassiz (1833) considered in his time *Amblypterus eupterygius* to be close to *Amblypterus macropterus*. He saw the differences between these two species in outer proportions of the body (more elongated trunk, less arched dorsal region of the body, proportionally larger peduncle of the caudal fin, large head more elongated and inconspicuously passing to the trunk, the dorsal fin shifts more anteriorly in *A. eupterygius*). Agassiz (1833, Pl. 3, Figs 5, 6) figured two specimens of *A. eupterygius* which are preserved: specimen VP 1364 (Fig. 6) figured by Agassiz (1833, Fig. 6) is deposited in the collection of the Université de Strasbourg, the specimen SMNS 95379 figured by Agassiz (1833, Fig. 5) is deposited in the collection of Staatliches Museum für Naturkunde, Stuttgart (Fig. 7). The specimen VP 1364 from Strasbourg was later studied and figured by Heyler (1976, Fig. 7, Photos 5, 6), who determined it as *Watsonichthys eupterygius* (Agassiz, 1833-43) = *Elonichthys pectinatus* Traquair, 1877 = *Watsonichthys pectinatus* (Aldinger, 1937).

Both specimens figured by Agassiz (1833) are relatively small. Specimen VP 1364 has the head partly preserved besides the anterior region, the posterior part of the caudal fin is missing. If it were whole, its total length would be no more than 170 mm. Specimen SMNS 95379 lacks posterior part of the dorsal and ventral lobes of the caudal fin, and its overall length does not exceed 95 mm. Both specimens exhibit the fusiform shape of the body, not arched dorsally. The length of the head is 4.7 times (SMNS 95379), 4.3 times (VP 1364) the total length of the fish. Very large pectoral fin of both specimens reaches the leading edge of the pelvic fin. Twenty articulated lepidotrichia comprise the pectoral fin (VP 1364). A few segments of the lepidotrichia are very long on SMNS 95379. The longest lepidotrichia comprise only eight segments, and it is an indication of a very young specimen. The pelvic fin (SMNS 95379) comprising 21 lepidotrichia is situated approximately in the middle of the total length of the fish, its base is close to the ventral margin of the body. The dorsal fin is large and triangular, the posterior margin of the fin is straight. It comprises 38 articulated lepidotrichia (SMNS 95379), and the distally pointed terminal segments protect the leading edge of the fin. The endoskeleton of the dorsal fin form the stick-like radials with their broad proximal and distal ends. Radials are arranged in one line. The specimen SMNS 95379 exhibits 13 anteriorly arranged radials which are equivalent to 17 anteriorly placed lepidotrichia. The anal fin is of triangular shape, large,

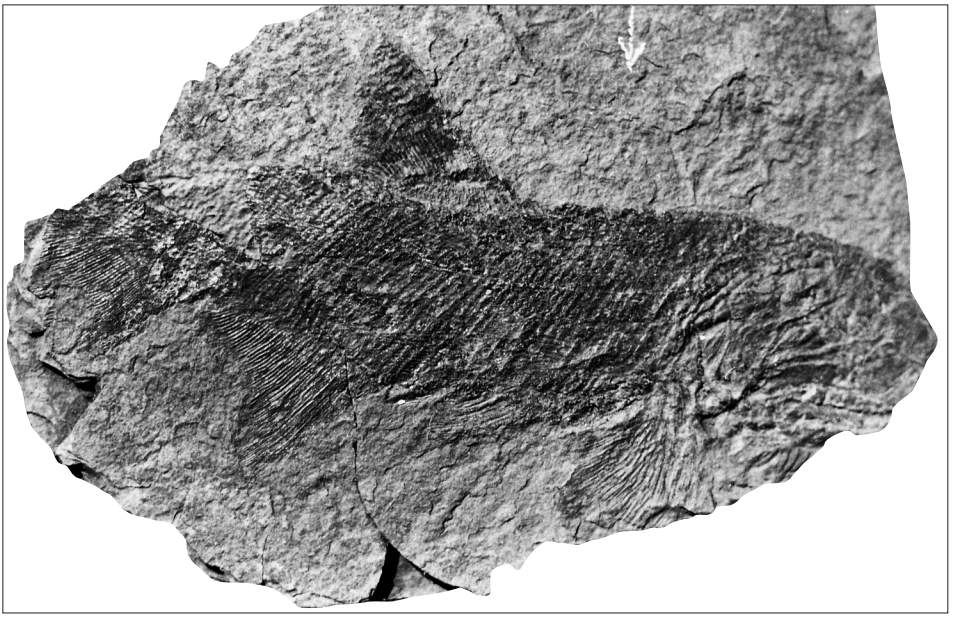

Fig. 6. *Rhabdolepis eupterygius* (Agassiz, 1833). Type specimen VP 1364, × 0.7.

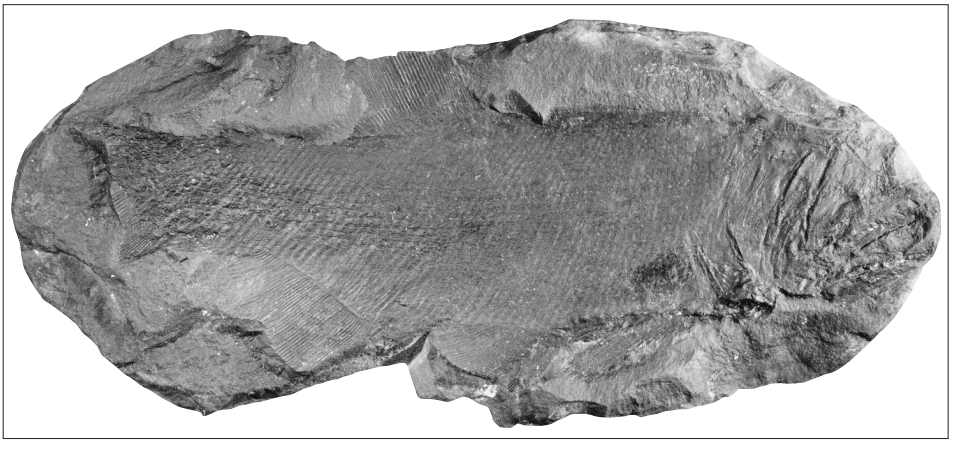

Fig. 7. *Rhabdolepis eupterygius* (Agassiz, 1833). Type specimen SMNS 95379, × 1.2.

with concave posterior margin. It is composed of 48 lepidotrichia on both specimens. The length of the bases of the anal and dorsal fins are the same in specimen SMNS 95379, or the base of the anal fin is one third longer than the base of the dorsal fin in specimen VP1364. The anal and dorsal fins are in outline well preserved in VP 1364, and the anal fin is apparently larger than the dorsal one (Fig. 6). The 13 anteriorly placed radials of the endoskeleton of the anal fin are well preserved on SMNS 95379 (Fig. 8). They have broad basal plate and narrow and long antero-dorsally oriented processus. 35 anteriorly

Fig. 8. ***Rhabdolepis eupterygius*** **(Agassiz, 1833). Lepidotrichia and radials of the anal fin, SMNS 95379, × 3.**

situated lepidotrichia are equivalent to 13 radials. The posteriorly situated radials are not preserved.

The thick, small and distinctively sculptured scales form the squamation. The scales cannot be counted on VP 1364. The scale count on SMNS 95379 is:

$$\frac{35}{10\ \ 29\ \ 57}?$$

From eight to nine scales are in the fifteenth scale row superiorly to the lateral sensory line, and 17 scale inferiorly to the lateral sensory line. The striae on the outer surface of the scale run from the anterior-superior corner to the posterior-inferior corner, but a little less steeply than the direction of diagonal. The striae anastomose occasionally posteriorly and they terminate as denticulation on the posterior margin of the scales. The scales on the flank in anterior region of the body are of oblong shape, they have six striae, and the number of striae decreases on the scales lying posteriorly and the shape of the scales becomes rhombic. The striae are well developed also on the scales of the caudal peduncle. The scales on the ventral region of the flank are anteroposteriorly elongated.

Maxilla is partly preserved on VP 1364 only, and it shows low and long maxillary plate. Lower jaw is strong. Teeth are observable on none of studied specimens. The preopercular is bent anteriorly with broad anterior region. Probably two suborbital bones lay anteriorly to the preopercular. The hyomandibular with processus opercularis is also bent anteriorly, and anterior and ventral branches form together angle 147° (VP 1364) or 155° (SMNS 95379). The opercular is high and narrow (Fig. 5D). It is the widest dorsally and narrowing ventrally. The bones ventrally to the opercular are preserved on none of the specimens, and information about this region of the skull is sketchy. The branchiostegal rays are probably numerous and narrow, and their fragments occur ventrally to the lower jaw. The supracleithrum is dorsoventrally conspicuously elongated similarly to the opercular.

On the basis of the above enumerated features of *R. eupterygius*, namely the shape of the body, very large pectoral fin, the shape and size of the unpaired fins, the sculpture on the scales, the scale count, upper jaw with low and long maxillary plate, the shape of the hyomandibular, the shape of the opercular I suggest that *R. eupterygius* is not a separate species, but a young specimen of *Rhabdolepis macropterus*. The determinative features mentioned by Agassiz (1833) are a consequence of the preservation and deformation in the course of fossilization, and not characters of a separate species.

RELATIONSHIPS OF *RHABDOLEPIS* TO SOME SPECIES FROM THE LATE CARBONIFEROUS OF BOHEMIA

Several important features listed for *Rhabdolepis* are known also from two species from the Upper Carboniferous of the Bohemia. They were described initially by Fritsch (1895) as *Acrolepis krejčii* and *Acrolepis sphaerosideritarum*. Štamberg (1991) included them in the genera *Watsonichthys* and "*Elonichthys*" (Štamberg 2006, Štamberg & Zajíc 2008), respectively. The study of specimen M 109 (Figs. 9, 10) and other fragmentary material newly discovered in the collection of the Museum of Western Bohemia at Plzeň supports my view that all represent a single species. The features distinguishing these two species (Fritsch 1895, Štamberg 1991) are a consequence of various degrees of deformation and not species distinctions. For that reason, I consider valid the species initially described by Fritsch (1895) as *Acrolepis krejčii* and most recently as "*Elonichthys*" *krejcii* by Štamberg & Zajíc (2008). I consider *Acrolepis sphaerosideritarum* Fritsch, 1895 to be a synonym of the former species.

The conspicuous coincident features on *Rhabdolepis* and "*Elonichthys*" *krejcii* are at first sight the shape of the opercular, presence of the presupracleithrum, very large pectoral fin, the sculpture on the scales. The antopercular squeezes between the dorsal margin of the preopercular, and the anterior margin of the opercular is dorsoventrally elongated. The type specimen of "*Elonichthys*" *krejcii* together with specimen M 109 exhibits, after thorough study, the following characters clearly distinguishing it from *Rhabdolepis*.

1. Configuration of the skull roof. Gardiner (1963, Fig. 9) figured in *Rhabdolepis macropterus* long dermopterotic boarding the parietal and frontal, and the dermosphenotic situated between the anterior region of the dermopterotic and the orbit. "*E.*" *krejcii* exhibits on the contrary a short dermopterotic anteriorly bordering with the dermosphenotic, and then the boundary of both bones is at the level of the parietal and frontal boundary (Fig. 10). The infraorbital canal continues from the dermopterotic to the dermosphenotic where it divides into two branches on "*E.*" *krejcii*. One branch of the infraorbital canal bents ventrally and it continues alongside the posterior margin of the orbit. The second branch traverses along the dorsal border of the orbit up to anterior region of the dermosphenotic.
2. Configuration of the opercular apparatus. The opercular of "*E.*" *krejcii* conspicuously narrows ventrally. This feature may seem to be different from the reconstruction of *R. macropterus* presented by Gardiner (1963, Fig. 9). The parallelogram shaped opercular figured by Gardiner (1963, Fig. 9) occurs in the type species of *R. saarbrueckensis* (BMNH 32576), and the same shape observed Schindler (personal communication) in some other specimens of *R. macropterus*. However, I found the opercular narrowing ventrally in the specimen Sc 95 of *R. saarbrueckensis* (Fig. 3, Fig 5D), in the type specimen BMNH P3453 of *R. macropterus* (Fig. 5A), in the specimen BMNH P6196 of *R. macropterus* (Fig. 5B), and on the both types of *R. eupterygius* (Fig. 5D). A fundamental difference is in the shape of the accessory opercular. *Rhabdolepis* has ventrally to the opercular one or two accessory operculars of oblong shape separating completely the opercular from the subopercular. Small and numerous branchiostegal rays follow ventrally from the subopercular. „*E.*" *krejcii* to the contrary exposes the subopercular nearly square in shape ventrally to the opercular. Large branchioste-

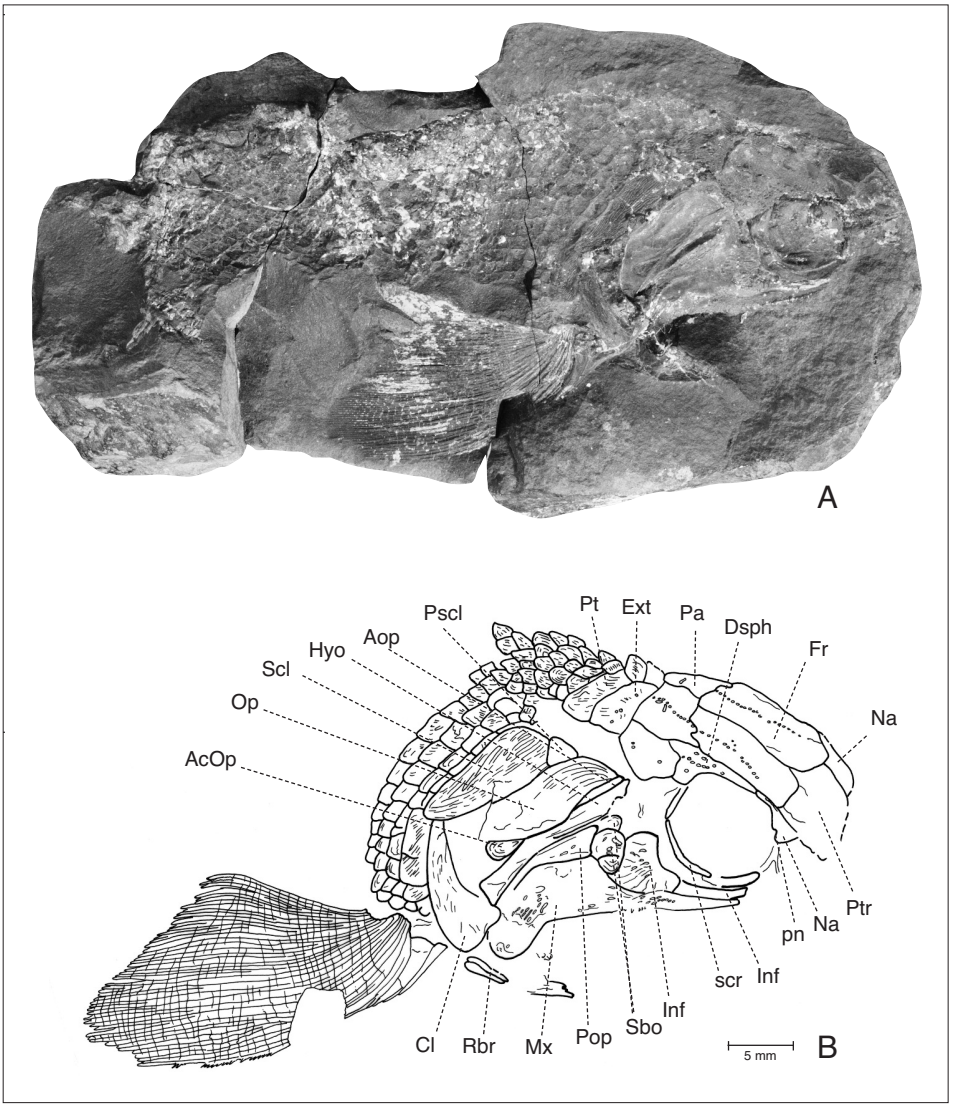

Fig. 9. "*Elonichthys*" *krejcii* (Fritsch, 1895). Specimen M 109 from the locality Malesice (Plzeň Basin, Stephanian B). A, photo of whole sample, × 1.4; B, interpretive drawing of the head and the pectoral fin. AcOp – accessory opercular; Aop – antopercular; Cl – cleithrum; Dsph – dermosphenotic; Ext – extrascapular; Fr – frontal; Hyo – hyomandibular, Inf – infraorbital; Mx – maxillary; Na – nasal; Op – opercular; Pa – parietal; pn – posterior naris; Pop – preopercular; Pscl – presupracleithrum; Pt – posttemporal; Ptr – postrostral; Rbr – branchiostegal ray; Sbo – suborbital; Scl - supracleithrum; scr – sclerotic ring; soc – supraorbital canal.

gal ray follows ventrally to the subopercular, and there are only subsequently other narrow branchiostegal rays. The triangular accessory opercular (epipreopercular in the sense of Štamberg 1991) squeezes in the space among the opercular, subopercular and preopercular (Fig. 9) in "*E.*" *krejcii*. Two accessory operculars of oblong shape completely separate the opercular from the subopercular in *Rhabdolepis*.

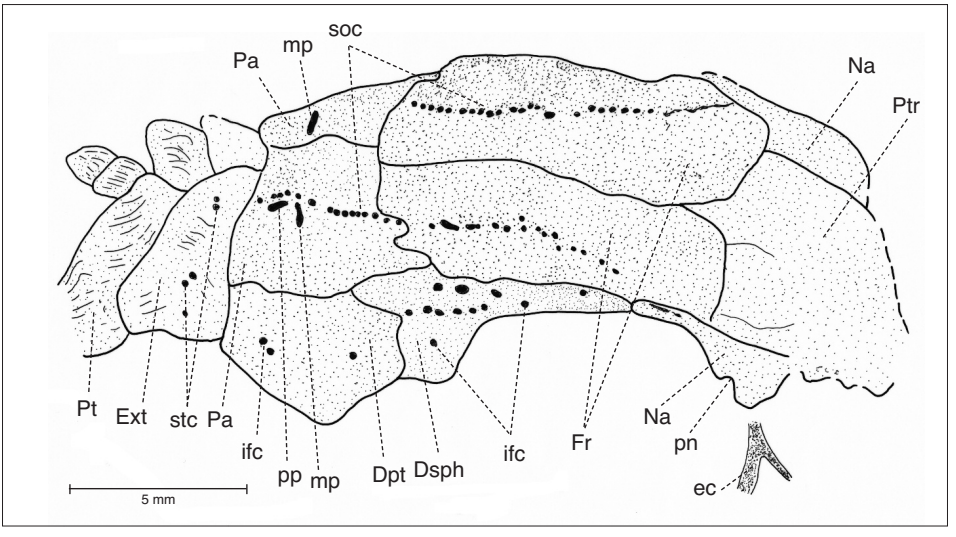

Fig. 10. "*Elonichthys*" *krejcii* (Fritsch, 1895). Drawing of the skull roof, M 109, × 5. Dsph – dermosphenotic; Dpt – dermopterotic; ec – ethmoidal commissure; Ext – extrascapular; Fr – frontal; ifc – infraorbital canal; mp – median pit line; Na – nasal; Pa – parietal; pn – posterior naris; Pt – posttemporal; Ptr – postrostral; pp – posterior pit line; Rbr – branchiostegal ray; Sbo – suborbital; Scl - supracleithrum; scr – sclerotic ring; soc – supraorbital canal; stc – supratemporal commissure.

The above mentioned characters clearly separate "*E.*" *krejcii* from *Rhabdolepis*, even though they look similar at first sight. Just the similarity of *Acrolepis krejcii* and *A. sphaerosideritarum* with *Rhabdolepis eupterygius* in the past led me (Štamberg 1991) to include them in the genus *Watsonichthys*, because Heyler's (1976) revision of the type material included *R. eupterygius* in *Watsonichthys*. A study of the type specimens of *Watsonichthys pectinatus* at the Royal Scottish Museum at Edinburgh later convinced me that the maxillary plate of *W. pectinatus* is conspicuously elongated and low, considerably as different from that of *R. eupterygius,* as from that of "*E.*" *krejcii*. Especially the significant difference in the shape of the upper jaw is the reason for removing "*E.*" *krejcii* from *Watsonichthys*.

The characters, which were listed as important for distinguishing "*E.*" *krejcii* and *Rhabdolepis* are on the contrary common for "*E.*" *krejcii* and *Meisenheimichthys* Schindler, 2004. There are many more shared features as follows:

1. The dermopterotic borders anteriorly with the dermosphenotic, and bordering of both bones is approximately at the level of the bordering of the frontal and parietal. Infraorbital canal traverses from the dermopterotic on the dermosphenotic where it divides to two branches. One branch bents ventrally along the posterior margin of the orbit, the second one continues anteriorly above the dorsal margin of the orbit.
2. The shape of the maxilla.
3. The hyomandibular with the processus opercularis and identical in the angle of the bend of the hyomandibular.
4. The opercular narrows ventrally, square shape subopercular, large first branchiostegal ray ventrally from the subopercular and much narrower remaining branchiostegal rays. The accessory opercular of triangular shape squeezes in among opercular, subopercular and preopercular.

5. There is a presupracleithrum between the dorso-posterior margin of the opercular and dorso-anterior margin of the supracleithrum.
6. Position of the paired and unpaired fins.
7. Very large pectoral fin.

Several above mentioned characters speak volumes for the close connection between "*E*." *krejcii* and *Meisenheimichthys* in the sense of Schindler (1993, 2004, 2007). I see important differences in the form of the bones of the skull roof dorsally from the orbit. *Meisenheimichthys* is characterized by anteriorly elongated dermosphenotic, but this bone does not reach the nasal, and the frontal forms the border of the orbit. The samples of "*E*." *krejcii* demonstrate the dermosphenotic anteriorly elongated and reaching the posterior margin of the nasal. The dermosphenotic and the nasal completely separate the frontal from the orbit. The same configuration of the bones shows *Rhabdolepis saarbrueckensis* (Fig. 3). The study of the specimens of the genera *Rhabdolepis* and *Meisenheimichthys* and of "*E*." *krejcii* makes clear that among these species are closely related to each other, and simultaneously specifies important differences. Therefore I tentatively place "*E*." *krejcii* in the genus "*Elonichthys*" and in the family Elonichthyidae in the sense of Schindler (2004).

CONCLUSIONS

Study of a second specimen of *Rhabdolepis saarbrueckensis* Gardiner, 1963, together with the restudy of the type specimen improved the description of the species. The bones of the cheek together with the hyomandibular, the axial skeleton, the endoskeleton of the dorsal and anal fins, the scale count of *R. saarbrueckensis* were described, and characters distinguishing *R. saarbrueckensis* from *R. macropterus* were corroborated.

The types and referred material of *R. macropterus* and *R. saarbrueckensis* show that the shape of the opercular is variable. The opercular is either wider in its dorsal region and narrower ventrally or it is parallelogram shaped. A restudy of the type specimens of *R. eupterygius* showed that the characters on whose basis Agassiz (1833) distinguished *R. macropterus* from *R. eupterygius* are a consequence of the preservation and deformation in the course of fossilization, and not specific characters. I consider both type specimens of *R. eupterygius* to be young individuals of *R. macropterus*.

The newly described material from the Late Carboniferous of the Central Bohemian Basins showed that "*Elonichthys*" *sphaerosideritarum* is a synonym of "*Elonichthys*" *krejcii,* and that it exhibits important features (configuration of the skull roof and opercular apparatus) distinguishing this species from *Rhabdolepis*. The shape of the maxilla is an important character showing that "*Elonichthys*" *krejcii* does not belong in the genus *Watsonichthys*. I found striking similarity between "*Elonichthys*" *krejcii* and the genus *Meisenheimichthys*, namely in the construction of the part of the skull roof, cheek bones and maxilla, opercular apparatus, pectoral fin and position of the fins. The fundamental difference is in the mutual position of the dermosphenotic, the frontal and the nasal. I provisionally placed "*Elonichthys*" *krejcii* in the genus *Elonichthys* of the family Elonichthyidae.

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REFERENCES

Agassiz L., 1833: Recherches sur les Poissons fossiles. Vol. 2. – Neuchâtel: L. Agassiz, xii + 336 pp.

Aldinger H., 1937: Permische Ganoidfische aus Ostgrönland. – Meddelelser øm Gronland 102(3): 1-392.

Arratia G. & Schultze H.-P., 1991: Palatoquadrate and its ossifications: development and homology within osteichthyans. – Journal of Morphology 208: 1-81.

Boy J.A., 1976: Überblick über die Fauna des saarpfälzischen Rotliegenden (Unter-Perm). – Mainzer Geowissenschaftliche Mitteilungen 5: 13-85.

Boy J.A., 1994: Seen der Rotliegend-Zeit – Ein Lebensraum vor rund 300 Millionen Jahren in der Pfalz. – In: Koenigswald W. & Meyer W. (eds.): Erdgeschichte im Rheinland. Fossilien und Gesteine aus 400 Millionen Jahren: 107-116. München: Pfeil Verlag.

Bronn H.G., 1829: Ueber die Fisch-Abdrücke in Eisenstein-Nieren des mittel-Rheinischen Steinkohlen-Gebirges, und über *Palaeoniscum macropterum* n. sp. insbesondere. – Zeitschrift für Mineralogie 2: 483-494..

Cope E.D., 1877: On the classification of the extinct fishes of the lower types. – Proceedings of the American Association for the Advancement of Science 26: 292-300.

Fritsch A., 1895: Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. Vol. 3 (Heft 4). – Praha: F. Hřivnáč, pp. 105-132.

Gardiner B.G., 1963: Certain Palaeoniscoid fishes and the evolution of the snout in Actinopterygians. – Bulletin of the British Museum (Natural History), Geology 8: 257-325.

Giebel C.G., 1848: Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere Vol. 1. Wirbelthiere. 3. Fische. Leipzig: F. A. Brockhaus, 467 pp.

Giebel C.G., 1849: Fischüberreste. – In: Germar E.F. (ed.): Die Versteinerungen des Steinkohlengebirges von Wettin und Löbejün im Saalkreise 6: 69-79. Halle: C. A. Schwetschke und Sohn.

Goldfuss G.A., 1847: Beiträge zur vorweltlichen Fauna des Steinkohlengebirges. Bonn: [s.n.] 26 pp.

Grande L. & Bemis W., 1998: A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. – Journal of Vertebrate Paleontology 18, Supplement Memoirs (1-4): 1-690.

Heyler D., 1976: Sur le genre *Amblypterus* Agassiz (Actinoptérygien du Permien inférieur). – Bulletin de la Sociéte d'Histoire Naturelle d'Autun 78: 17-37.

Nielsen E., 1942: Studies on Triassic fishes from East Greenland. I. *Glaucolepis* and *Boreosomus*. – Palaeozoologica Groenlandica 1: 1-403.

Poplin C.M. & Véran M., 1996: A revision of the actinopterygian fish *Coccocephalus wildi* from the Upper Carboniferous of Lancashire. – In: Milner A.R. (ed.): Studies on Carboniferous and Permian vertebrates. Special Papers in Paleontology 52: 7-29.

Poschmann M. & Schindler T., 2004: Sitters and Grügelborn, two important fossil-Lagerstaetten in the Rotliegend (?Late Carboniferous – Early Permian) of the Saar-Nahe Basin (SW-Germany), with the description of a new palaeoniscoid (Osteichthyes, Actinopterygii).– Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 232: 283-314.

Sauvage H.E., 1888: Poissons du terrain houiller de Commentry. – In: Fayol M. (ed.): Études sur le terrain houiller de Commentry. Vol. 3: 39-120. Saint-Étienne.

Schindler T., 1993: "*Elonichthys*" *palatinus* n. sp. a new species of actinopterygians from the Lower Permian of the Saar-Nahe Basin (SW-Germany). – In: Heidtke U.H.J. (ed.): New research on Permo-Carboniferous faunas. – Pollichia-Buch 29: 67-81. Bad Dürkheim.

Schindler T., 2007: Knochenfische (Osteichthyes). Die häufigsten Wirbeltiere permocarbonischer Seen. – In: Schindler T. & Heidtke U.H.J. (eds): Kohlesümpfe, Seen und Halbwüsten. Pollichia Sonderveröffentlichung 10: 240-256. Bad-Dürkheim.

Štamberg S., 1983: Revision of the genus *Sceletophorus* (Actinopterygii) from the Carboniferous of the Plzeň Basin. – Acta Musei Reginaehradecensis S.A. 18: 43-74.

Štamberg S., 1991: Actinopterygians of the Central Bohemian Carboniferous Basins. – Acta Musei Nationalis Pragae (B) 47: 25-104.

Štamberg S., 2006: Carboniferous/Permian actinopterygian fishes of the continental basins of the Bohemian Massif, Czech Republic – an overview. – In: Lucas S.G., Cassinis G. & Schneider J.W. (eds): Non-marine Permian biostratigraphy and biochronology. Geological Society of London, Special Publications 265: 217-230.

Štamberg S., 2007: Permo-Carboniferous actinopterygians of the Boskovice Graben. Part 1. *Neslovicella, Bourbonnella, Letovichthys, Elonichthys*. – Hradec Králové: Museum of Eastern Bohemia at Hradec Králové, 155 pp.

Štamberg S. & Zajíc J., 2008: Carboniferous and Permian faunas and their occurrence in the limnic basins of the Czech Republic. – Hradec Králové: Museum of Eastern Bohemia at Hradec Králové, 224 pp.

Traquair R.H., 1877: The ganoid fishes of the British Carboniferous formations. Part I. Palaeoniscidae. – Palaeontographical Society, Monographs, 31 (4): 1-60. London.

Troschel F.H., 1857: Beobachtungen über die Fische in den Eisennieren des Saarbrücker Steinkohlengebirges. – Verhandlungen des Naturhistorischen Vereines der Preussischen Rheinlande und Westphalens 14: 1-19.

Woodward A.S., 1891: Catalogue of the fossil fishes in the British Museum (Natural History). Vol. 2. London: British Museum (Natural History), 567 pp.